

Cross-scale variation in top-down and bottom-up control of algal abundance

Tess L. Freidenburg^a, Bruce A. Menge^{a,*}, Patti M. Halpin^b,
Michael Webster^c, Ariana Sutton-Grier^d

^a Department of Zoology, Oregon State University, Corvallis, OR 97331-2914, United States

^b Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, CA 93106, United States

^c Gordon and Betty Moore Foundation, San Francisco, CA 94129, United States

^d University Program in Ecology, Nicholas School of the Environment, Box 90328, Duke University, Durham, NC 27708, United States

Received 20 January 2007; accepted 19 February 2007

Abstract

Previous studies of top-down and bottom-up effects in Oregon rocky intertidal communities suggested that, unlike sea star–mussel dominated food chains, grazer–alga food chains deviated from simple food web predictions. However, this conclusion lacked generality due to limited replication at the site level. We explored how grazing and algal colonization and growth in different zones and multiple sites in intertidal communities varied in relation to processes varying on local to mesoscales, including oceanographic variation. Our approach employed the comparative-experimental method, in which identically-designed and replicated experiments are performed at multiple sites spanning the environmental gradient of interest. In a limpet–algae–barnacle interaction web, we tested the hypothesis that top-down and bottom-up effects were inversely related along the Oregon coast. To distinguish between the alternatives of large-scale oceanographic forcing vs. local control, our experiments spanned scales of meters (between mid and low zones), kilometers (seven sites), 10's to 100's of km (three regions), and ~ 260 km (central and southern coasts). Identically designed and executed experiments on effects and rates of grazing were conducted in a southern coast region of persistent upwelling and two central coast regions, one with intermittent upwelling in an area of weak offshore currents, and another with intermittent upwelling in an area of strong offshore currents. Grazer effects and grazing rates varied on all scales, indicating a complex interplay of processes operating at zone, site, regional, and coastal scales. Grazing was generally highest in all mid zones and in the low zone at the middle region (Cape Perpetua) on the central coast. Growth of early successional colonists tended to be higher at the northern and southern regions (Capes Foulweather and Blanco). Grazers had no effect on barnacle cover, but their foraging was inhibited by high densities of barnacles. Differences in grazing appear to be a complex consequence of direct and indirect effects of variable oceanographic conditions, limpet recruitment, and barnacle abundance. In contrast to positive associations between predation strength and the magnitude of prey subsidies, higher grazing strength was generally associated with lower magnitude of bottom-up effects and vice versa. Hence in this system predator–prey (sea star–filter feeder) and herbivore–plant (limpet–microalgae) interactions evidently respond differently to ecological subsidies.

© 2007 Published by Elsevier B.V.

Keywords: Algae; Bottom-up; Community structure; Early succession; Ecological subsidies; Grazing; Oregon; Rocky intertidal; Species interactions; Top-down; Upwelling

* Corresponding author.

E-mail address: mengeb@oregonstate.edu (B.A. Menge).

1. Introduction

Since Hairston et al. (1960) proposed a top-down model of community regulation, ecologists have debated whether predation or primary productivity is most important in determining community structure and dynamics (Oksanen et al., 1981; Fretwell, 1987; Polis, 1999; Polis et al., 2000; Schmitz et al., 2000; White, 2001). However, in recent years ecologists have increasingly adopted an integrated perspective that recognizes the dynamic linkage between top-down and bottom-up processes (Hunter and Price, 1992; Menge, 1992, 2003, 2004; Menge et al., 1997a; Fraser, 1998; Leonard et al., 1998; Nielsen, 2001, 2003; Menge et al., 2003; Thompson et al., 2004). Determining the relative importance of, and linkages between, top-down and bottom-up processes is crucial to understanding variation in community structure.

Studies in marine intertidal systems have been fruitful in exploring the relative contributions of top-down and bottom-up processes. In South Africa, increases in nutrient supply from bird guano modified community structure through enhancement of algal production, leading to increased growth of limpets and greater abundance of algal-dwelling invertebrates (Bosman et al., 1986; Bosman and Hockey, 1986). Invertebrates associated with the algal turf in areas with inputs of guano provided food for small shorebirds. In unenriched areas, algal mats and their associated communities of invertebrates and shorebird predators were absent. In New England, differences in flow velocity influenced the delivery of subsidies such as nutrients, food and larvae to intertidal habitats (Leonard et al., 1998, 1999). In high flow environments, subsidy effects were stronger due to both higher delivery rates of planktonic larvae and food and to inhibition of foraging by predatory crabs. In low flow environments, consumer effects were stronger as foraging rates of crabs increased with reduced hydrodynamic forces.

1.1. Background

Research on the Oregon coast indicates that top-down effects (i.e. predation and grazing) and ocean-derived subsidies (i.e., phytoplankton concentrations and prey recruitment) affect intertidal community structure (Menge, 1992; Menge et al., 1994; Menge et al., 1997a; Menge, 2000). However, the magnitude of these effects differed substantially between two sites. Boiler Bay (hereafter BB) and Strawberry Hill (hereafter SH), 80 km apart on the Oregon coast, have contrasting patterns of community structure in the low intertidal

zone. BB has a high cover of algae and low cover of sessile invertebrates while SH has the opposite (Menge, 1992; Menge et al., 1994). Observational and experimental studies have demonstrated that at SH, where phytoplankton productivity and recruitment rates were consistently higher, predation and grazing rates were also higher (Menge et al., 1997a; Menge, 2000). The greater top-down forces and subsidies at SH are thought to depend on differences in nearshore (0–10 km from shore) oceanographic patterns (Menge et al., 1997a,b).

Previous studies in Oregon have led to a seeming paradox (Menge, 2000). While both predation and grazing were strongest at SH, their association with their respective subsidies contrasted. As expected from simple food chain theory (Oksanen et al., 1981), mussels and barnacles, the primary prey of sea stars and whelks, were generally more abundant at SH, where predation was strong. The dynamics of the limpet–algal food chain, however, seemed more consistent with a simple top-down perspective. Benthic algae, the primary food resources of limpets, were generally less, not more, abundant at SH. Classically, inverse relationships between resource and consumer abundance have suggested that consumers were responsible for the low resource abundance (e.g., Hairston et al., 1960). The observation that field measurements of macroalgal (*Saccharina* [formerly *Hedophyllum*] *sessile*) growth did not differ between BB and SH (B. A. Menge, unpublished data) seemed consistent with this hypothesis. Thus, the interaction web topped by limpets evidently exhibited qualitatively different dynamics, suggesting that nutrient–macrophyte based interaction webs and nutrient–phytoplankton based interaction webs respond differently to oceanographic conditions. These studies were limited to a comparison between two sites, however, so whether these results were general, i.e., representative of larger, coast-wide patterns, was unclear.

1.2. Oceanographic scenario

As has recently been demonstrated for the sea star–filter feeder interaction web (Menge et al., 2004), regional differences in consumer effects and resource subsidies may stem from variability in the intensity of seasonal upwelling. A summary of key coastal oceanographic features characterizing the Oregon coast can be found in Menge et al. (2004). Briefly, on the US West Coast seasonal upwelling occurs during spring and summer when equatorward winds, combined with the Coriolis effect, drive surface water offshore. Displaced surface water is replaced by cold, nutrient-rich water from depth (Parrish et al., 1981; Brink, 1983; Huyer,

1983). Nutrient-laden upwelled water fuels the growth of phytoplankton and macrophytes. Upwelling-induced phytoplankton blooms can have several effects, including direct bottom-up (food) effects on growth of filter-feeding invertebrates (Menge, 1992; Menge et al., 1994, 2004; Dahlhoff and Menge, 1996; Sanford and Menge, 2001) and their larvae and recruits (Phillips, 2002; Phillips and Gaines, 2002). Bottom-up phytoplankton effects indirectly may influence macrophyte communities if fast-growing sessile invertebrates preempt space or inhibit grazers (Dungan, 1986; Farrell, 1991). Another direct and underappreciated potential bottom-up effect of phytoplankton blooms is shading of macrophytes. Recent studies (Nielsen et al., in preparation, Kavanaugh et al., in preparation) suggest that coastal blooms can be so dense that at high tide light is completely attenuated in the low intertidal zone. A final, more traditional bottom-up effect is elevated macrophyte growth from high nutrient inputs causing an increase in grazer density and thus increasing top-down impacts (Bustamante et al., 1995a,b).

Seasonal upwelling varies in intensity along the west coast of North America in response to both latitude and local geographic features. The Coriolis effect weakens at higher latitudes reducing offshore transport of surface water (Mann and Lazier, 1996). Upwelling intensity does not decrease gradually with increased latitude, but is locally strengthened near major headlands where upwelling favorable winds intensify and the California Current is deflected offshore (Parrish et al., 1981; Brink, 1983; Smith, 1983; Rosenfeld et al., 1997). Thus the coast is comprised of distinct upwelling regions bounded by oceanographic discontinuities (Parrish et al., 1981). One such discontinuity is Cape Blanco (CB) on the southern Oregon coast (e.g., Menge et al., 2004) (Fig. 1). North of CB, upwelling is relatively intermittent while at CB and southward, upwelling is more persistent (Parrish et al., 1981) (Fig. 2). Here we define “intermittent” upwelling as upwelling patterns that alternate on a relatively regular basis between upwelling and downwelling, with periods of each ranging between 3–14 days throughout the April–September upwelling season (Menge et al., 2004; Kosro, 2005). “Persistent” upwelling refers to patterns in which upwelling periods are longer (weeks) with fewer and briefer downwelling periods (a few days to a week) during the upwelling season.

Within an upwelling region, local differences in bathymetry and continental shelf width also may have important ecological consequences (Menge et al., 1997a, 2004). At Cape Foulweather (which includes BB), the continental shelf is narrow so the upwelling front is ~ 3–5 km offshore (Kosro 2005). At Cape

Perpetua (which includes SH), the shelf widens and the upwelling front is typically ~ 10–15 km from shore. Between the front and shore on this wider shelf region, eddies form that can concentrate or retain nutrients, phytoplankton and larvae (Menge et al., 1997a; Kosro et al., 1997; Kosro, 2005; Barth et al., 2007). Currents off Cape Foulweather tend to be stronger and more persistently southward than at Cape Perpetua, where currents are both weaker and more variable in direction (Kosro et al., 1997; Kosro, 2005). Differences in community structure and dynamics between these areas have been attributed in part to this mesoscale variation in nearshore currents (Leslie et al., 2005; Menge et al., 1997a,b, 2004; Menge, 2000, 2003).

1.3. Research goals

Our goals in the present study were to test alternative perspectives of top-down and/or bottom-up control. We did this by: (1) evaluating spatial and temporal variation in top-down effects of limpet grazers, (2) quantifying the response of colonizing benthic microalgae, and (3) examining how early successional algae responded to grazing across a nested series of spatial scales and associated oceanographic and ecological conditions.

Scaling up in ecology can often impose limitations that restrict interpretations of results. For example, large-scale studies often must sacrifice the strong inference allowed by experimentation because of logistical limitations imposed by working at large scales. The comparative-experimental approach, in which identically-designed and replicated experiments are carried out simultaneously at multiple locations or sites is one solution to these limitations (Dayton, 1971; Menge, 1991; Menge et al., 2002, 2003, 2004; Coleman et al., 2006). We used this approach to examine the response of the grazer–algae–barnacle interaction web to local, mesoscale and macroscale variation in environmental conditions. We compared the effects of grazers on early successional algae in mid and low zones, at seven sites, in three regions and two coastal sectors as described above. We focused on limpets because previous studies have documented the strong impact of limpets (e.g., *Lottia* spp., *Cellana* spp., *Patella* spp.) on intertidal algal assemblages (Branch, 1981; Castenholz, 1961; Cubit, 1984; Dayton, 1971; Farrell, 1991; Hawkins and Hartnoll, 1983; Menge, 2000; Underwood, 1980). We considered five questions: (1) Are patterns seen in earlier more limited studies in Oregon reflective of larger-scale limpet–algal dynamics? (2) How do top-down grazer effects and grazing rate vary at different spatial scales, including from smaller to larger, by zones, sites, regions

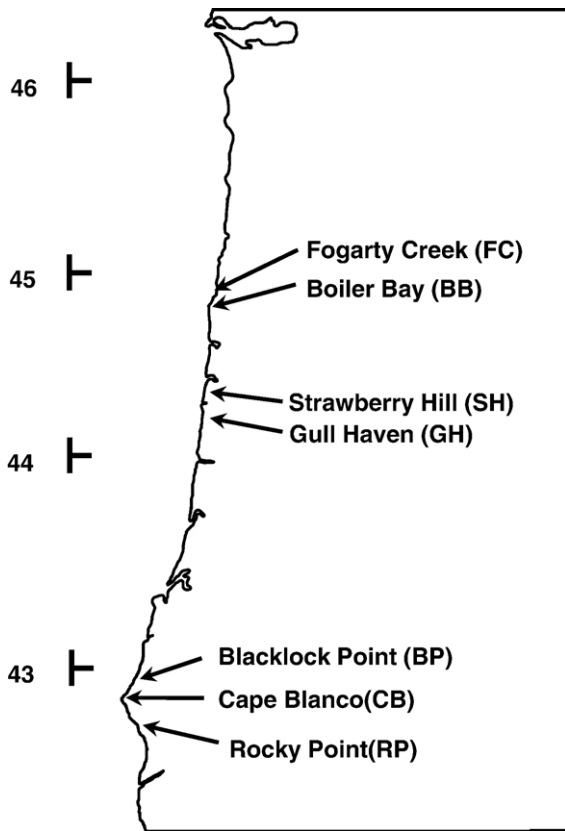


Fig. 1. Map of study sites along the Oregon coast. FC and BB are in the Cape Foulweather (CF) region, SH and GH are in the Cape Perpetua (CP) region and BP, CB and RP are in the Cape Blanco (CB) region.

and coasts? (3) How do interactions with barnacles influence the limpet–algal relationship? (4) What are the influences of bottom-up, oceanographic processes and other factors? And (5) which model best reflects the dynamics of this herbivore–plant system, top-down, bottom-up, or coupled top-down/bottom-up?

2. Methods

2.1. Study sites

We conducted grazing experiments at five sites in 1999 and seven sites in 2000. Sites ranged from Fogarty Creek (FC) on the central Oregon coast to Rocky Point (RP), 260 km to the south (Fig. 1). At each site we established experiments in areas that were similar in degree of wave-exposure, slope and aspect.

Two types of experiments tested the effect of herbivores on the early stages of colonization by benthic algae. In the *grazer effect* experiments we quantified the effect of grazers on recolonization of bare space. Because rates of

increase in algal cover can confound rates of grazing and algal growth, in the *grazing rate* experiments we measured how quickly grazers consumed algae after allowing a complete cover of algae to develop.

Hypothetically, limpet or algal composition differences among zones, sites or regions might underlie some of the differences summarized above. We discount this possibility for two reasons. First, our field observations suggest that the relative abundances of the main species in the limpet guild varied little by site or region. In low zone experiments, the limpets *Lottia pelta* and a small (~ 3–4 mm) unidentified species (termed *Lottia* sp.) were most abundant, while in mid zone experiments these species plus occasional individuals of *L. digitalis* and *L. strigatella*, normally more abundant in the high zone, made up the limpet guild. Second, at all sites early algal colonists consisted of chain-forming benthic diatoms and filamentous green algae (probably mostly species of *Ulothrix* and *Urospora*), while later-appearing algae were always a mix of *Enteromorpha* spp., *Petalonia fascia*, and *Scytosiphon simplicissimus*.

2.2. Grazer effect experiments

In both 1999 and 2000 we conducted grazer effect experiments in the low (~ 0 to + 0.5 m) and middle (~ + 1.0 to + 1.5 m) intertidal zones. Experiments began in June of each year and ended in August. In 1999 we used five sites: FC, BB, SH, GH and CB (Fig. 1). In 2000 we added two sites on the southern coast, BP and RP (Fig. 1).

Using an established design (e.g., Menge, 2000), we set up three treatments (exclusion, paint control, marked

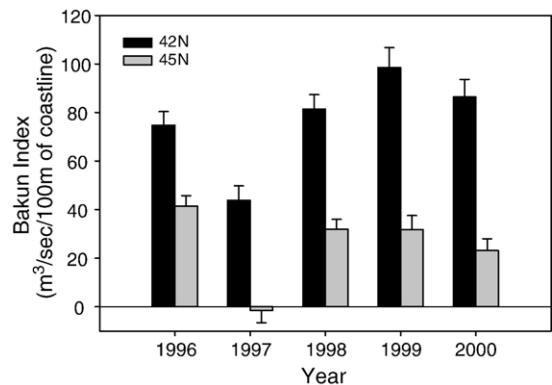
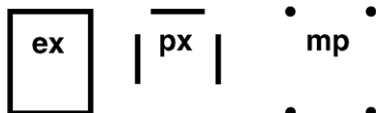


Fig. 2. Upwelling intensity as measured by the Bakun Index, which estimates the amount of water transported offshore. Positive values indicate upwelling favorable conditions while negative values indicate downwelling. The latitude 42° N is 93 km south of Cape Blanco and 45° N is 19 km north of Cape Foulweather and 83 km north of Cape Perpetua.

plot) in a randomized block design at each site (Fig. 3). In 1999 plots were approximately 20×30 cm, while in 2000 they were approximately 15×20 cm. To start the experiment we scraped each plot clear of benthic organisms manually and then applied oven cleaner (NaOH) to remove all the algae including algal crusts. Anti-limpet barriers were placed around each exclusion (coded as -limpet +paint) using copper anti-fouling paint coating a band of Z-spar, a marine epoxy putty (Z-spar™ Splash Zone Compound, Seattle Marine, Seattle, Washington, USA). Copper paint excludes limpets (Cubit, 1984; Paine, 1984; Menge et al., 1999; Menge, 2000, but see Benedetti-Cecchi and Cinelli, 1997 for a critique of this method), but not littorinid snails. Partial barriers (coded as +limpet +paint) gave limpets access to paint control plots and controlled for possible effects of copper paint on algal recolonization (Fig. 3). Unpainted Z-spar was used to mark the four corners of the marked plots (coded as +limpet -paint). In total, in 1999 there were 6 replicates \times 3 treatments \times 5 sites, or 90 plots, and in 2000 there were 5 replicates \times 3 treatments \times 7 sites \times 2 zones, or 210 plots.

After initiation, every two weeks we estimated the percent cover of dominant space occupiers (e.g., sessile organisms including algae, barnacles, mussels), counted limpets, and removed limpets invading exclosures. Since visual estimates are quicker and appear at least as accurate as estimates obtained using random dots or similar methods (Meese and Tomich, 1992; Dethier et al., 1993), percent cover was estimated visually directly in the field. Compared to marked plots and paint controls, relatively few invaders were found in exclosures, indicating that this method of excluding limpets was effective (e.g., mean number per plot \pm 1 se across all sites in 2000: low zone-exclosures, 2.3 ± 0.37 ; paint control, 33.7 ± 3.7 ; marked plot, 47.3 ± 4.55 , $n = 184$; mid zone-

A. Herbivore effect experiment



B. Herbivore rate experiment

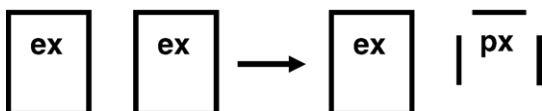


Fig. 3. Diagram of the experimental design. A. herbivore effect experiment (ex=full exclusion, pc=paint control, mp=marked plot) and B. herbivore rate experiment (ex=full exclusion, px=partial exclusion — after some of the initial barrier was removed).

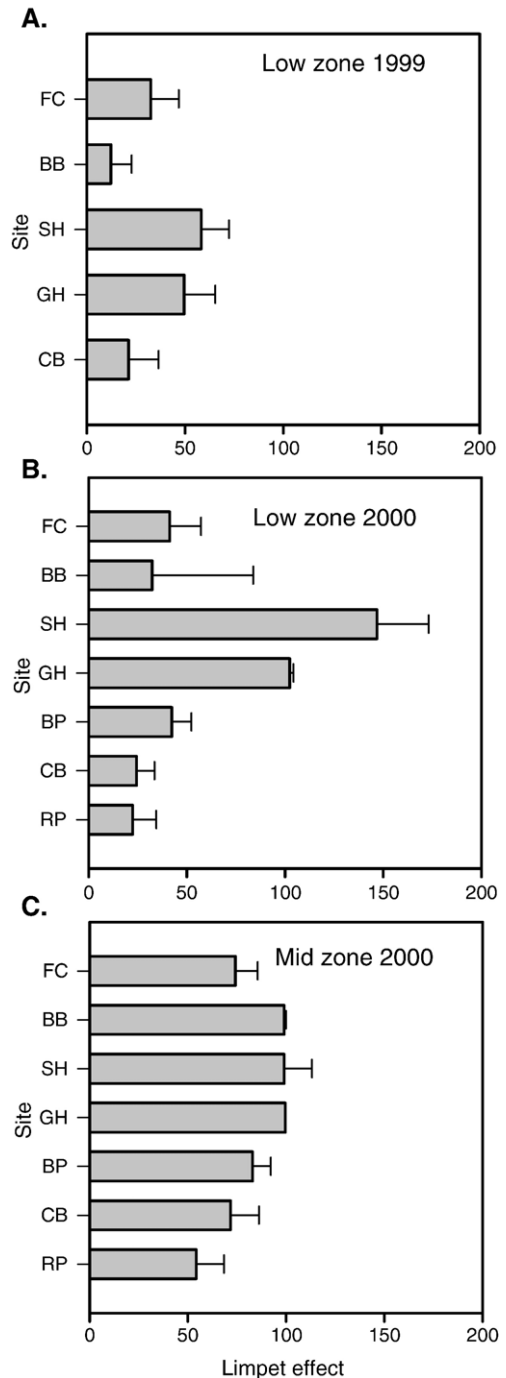


Fig. 4. The effect of limpets on the recolonization of bare space by algal sporelings and diatoms in (A) the low zone in 1999 (top panel), (B) the low zone in 2000 (middle panel) and (C) the mid zone in 2000 (bottom panel). In this and all subsequent figures, sites are arranged in latitudinal order with the FC, the northernmost, at the top and RP, the southernmost, at the bottom. The limpet effect is the difference in algal cover between the -limpet plots and the +limpet plots at the end of the experiment, which lasted 60 days in 1999 and 75 days in 2000.

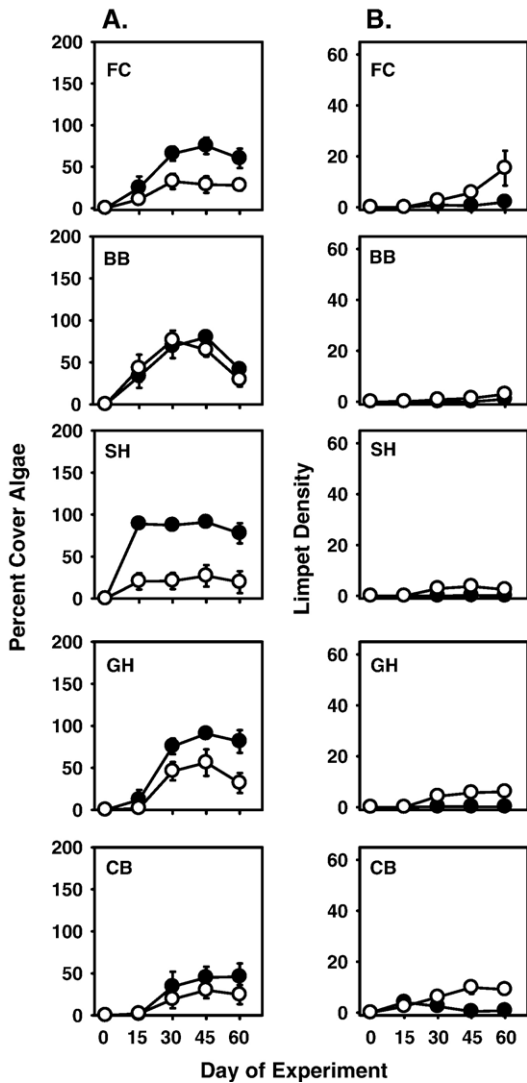


Fig. 5. Results of the low zone grazing effect experiment in 1999. Column (A) is the effect of limpets on the recolonization of bare space by algae, and column (B) is the density of limpets (grazers) over 60 days at five sites on the Oregon coast. Filled dots indicate -limpet treatment, open dots indicate +limpet treatments. Sites are arranged in latitudinal order with the northernmost site, FC, at the top and the southernmost site, CB, at the bottom. Error bars are 1 SE in this and all subsequent figures.

exclosures, 0.4 ± 0.10 ; paint control, 24.1 ± 2.3 ; marked plot, 33.6 ± 2.6 ; $n = 175$). We identified algae to species when possible, but often we could only identify functional groups (i.e. filaments, crusts, diatoms etc.).

2.3. Grazing rate experiments

We quantified the rate of grazing in the mid zone in 1999 and 2000 and in the low zone in 2000. In 1999 we

established experiments at three sites (BB, SH and CB) and in 2000 we repeated the experiments adding four more sites (FC, GH, BP, and RP; Fig. 1).

In 1999, mid zone grazing rate experiments consisted of eight pairs of 10×10 cm exclusions, with 8 replicates \times 2 treatments \times 4 sites, or 64 plots. After algal percent cover had increased to $\sim 100\%$ in most plots (ca. one month), we then randomly selected one plot from each pair and breached the barrier (removing about half), allowing limpets access (Fig. 3). The algal composition was similar in all plots prior to opening the barriers in both 1999 and 2000 experiments. Subsequent monitoring was identical to that in grazer effect experiments.

The 2000 mid and low zone grazing rate experiments were done in tandem with the effect experiments in each zone, which simply involved the addition of an extra exclusion plot, later to become the breached-barrier plot. Thus the grazer exclusion plot in the grazer effect experiment served as the control for the grazing rate experiment. All plots measured $15 \text{ cm} \times 20 \text{ cm}$, and in total there were 5 replicates \times 2 treatments \times 7 sites \times 2 zones, or 140 plots.

2.4. Statistical analysis

2.4.1. Grazer effect experiments

To test for paint-related artifacts, we compared the final percent cover of algae in paint control and marked plots using paired *t*-tests. As in previous experiments (e.g., Menge, 2000), there were no significant differences ($p > 0.05$) and we averaged covers in paint controls and marked plots as our +grazer response.

Three response variables were analyzed: total (non-crustose) algal cover, total barnacle cover and total limpet density. We tested the effect on algal cover of coast (central = CF and CP vs. southern = CB), region

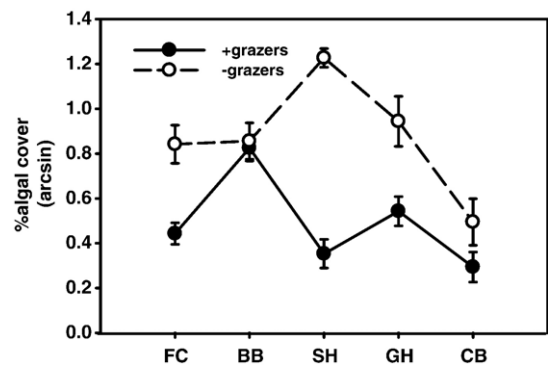


Fig. 6. Analysis of the site \times grazer interaction in the 1999 low zone grazing effect experiment showing arcsin-square root transformed data. Sites are arranged north to south, from left to right.

(CF = north, CP = central and CB = south), zone (mid and low) and grazing (+ and – limpets). The effect of site was tested as a main effect in 1999 and nested within region in 2000. Our response for barnacles was the average cover across all grazing treatments because cover did not vary among treatments in any of the experiments ($p > 0.20$). Copper paint was effective at excluding limpets at all sites, so we analyzed limpet density only in the +limpet treatments.

We used SYSTAT (v. 11.0) and JMP IN (v. 5.1) to analyze our data. We used repeated-measures ANOVA (RM-ANOVA; Crowder and Hand, 1990) in our analyses of algal and barnacle cover and limpet density. Repeated-measures analyses include univariate or

multivariate tests, the former of which is more powerful and is appropriate if assumptions of sphericity are met (von Ende, 1993). When this assumption was violated, we adjusted the probability using the more conservative Greenhouse–Geisser epsilon. For comparison we also present multivariate results, another conservative test. In nearly all cases, the conclusions from multivariate and univariate analyses were identical. Since repeated-measures ANOVA does not support random effects, all factors were fixed. We visually examined probability plots of residuals and plots of residuals vs. estimated values from univariate analyses to evaluate assumptions of normality and equal variance, respectively. When necessary, data were log transformed ($\ln [x + 1]$).

Table 1

Results of repeated-measures ANOVA testing the effect on algal cover ($\ln [x + 1]$) in 1999 (site and grazing as factors) and 2000 (region, zone and grazing as factors)

Univariate analysis					Multivariate analysis			
Source	<i>df</i>	MS	<i>F</i>	<i>p</i>	Wilks' λ	<i>df</i>	<i>F</i>	<i>p</i>
1999 Low zone								
Between subjects								
Site	4	2.2465	7.63	<0.0001				
Grazing	1	4.8777	16.57	0.0001				
Site*grazing	4	2.5120	8.53	<0.0001				
Error	71	0.2944						
Within subjects								
Time	3	0.1459	2.11	0.11	0.94771	3, 69	1.27	0.29
Time*site	12	0.2524	3.65	0.0003	0.62337	12,182	2.98	0.0008
Time*grazing	3	0.0673	0.97	0.39	0.94820	3, 69	1.26	0.30
Time*site*grazing	12	0.1886	2.73	0.005	0.69452	12,182	2.25	0.01
Error	213	0.0691						
2000 Low and mid zones								
Between subjects								
Region	2	9.6862	39.2	<0.0001				
Zone	1	13.7442	55.6	<0.0001				
Grazing	1	85.8528	347.5	<0.0001				
Region*zone	2	4.3598	17.6	<0.0001				
Region*grazing	2	5.0752	20.5	<0.0001				
Zone*grazing	1	5.2955	21.4	<0.0001				
Region*zone*grazing	2	2.1368	8.65	0.0003				
Site (region)	4	0.8985	3.64	0.007				
Error	194	0.2470						
Within subjects								
Time	4	2.6116	38.5	<0.0001	0.58078	4,191	34.5	<0.0001
Time*region	8	0.4617	6.80	<0.0001	0.79564	8,382	5.78	<0.0001
Time*zone	4	0.3225	4.75	0.0016	0.91492	4,191	4.44	0.002
Time*grazing	4	7.5473	111.2	<0.0001	0.32428	4,191	99.5	<0.0001
Time*region*zone	8	0.1547	2.28	0.027	0.91551	8,382	2.15	0.03
Time*region*grazing	8	0.4156	6.12	<0.0001	0.81179	8,382	5.25	<0.0001
Time*zone*grazing	4	0.5613	8.27	<0.0001	0.86486	4,191	7.46	<0.0001
Time*region*zone*grazing	8	0.2025	2.98	0.004	0.89752	8,382	2.65	0.008
Time*site (region)	16	0.7036	10.4	<0.0001	0.48740	16,584	9.68	<0.0001
Error	776	0.0679						

The sphericity test (Mauchly criterion) for multivariate normality failed in both analyses (1999: $\chi^2 = 30.5$, $p < 0.0001$; 2000: $\chi^2 = 65.6$, $p < 0.0001$), so we adjusted probabilities using the Greenhouse–Geisser epsilon (1999: 0.78988; 2000 0.87091).

For the data in bold, significance was at $p < 0.05$ or less.

We used linear contrasts to test four *a priori* hypotheses about differences among regions. Specifically, we examined differences between the southern (S) Oregon coast (region CB, sites BP, CB, and RP) vs. the central (C)

Oregon coast (region CF with sites FC and BB, and region CP with sites SH, GH), and all possible between-region comparisons (CF vs. CP, CF vs. CB, CP vs. CB). We determined if these models met assumptions of normality

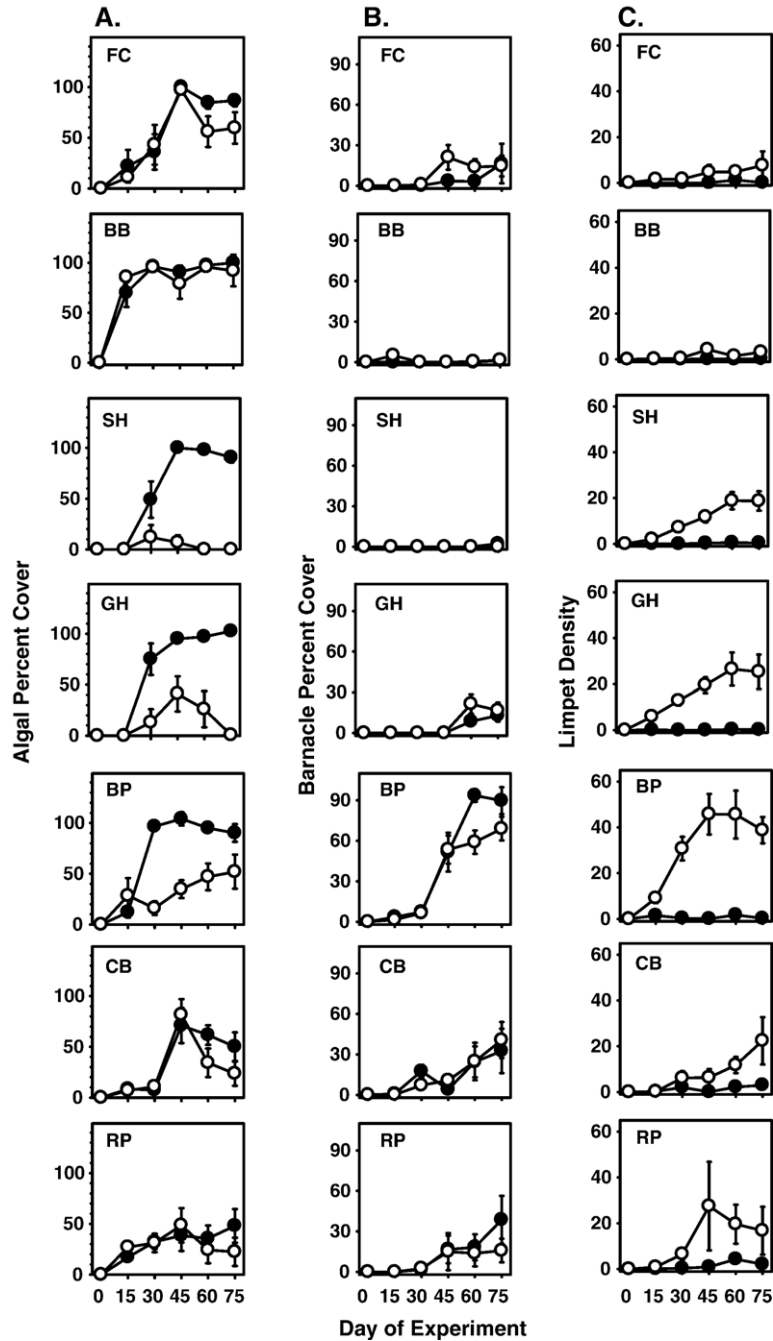


Fig. 7. Results of the low zone grazer effect experiment in 2000. Column (A) is the effect of limpets on the recolonization of bare space by algae, column (B) is the effect of limpets on the recolonization of bare space by barnacles and column (C) is the density of limpets (grazers) over 75 days at seven sites on the Oregon coast. Filled dots indicate -limpet treatment, open dots indicate +limpet treatments. Sites are arranged in latitudinal order with the northernmost site, FC, at the top and the southernmost site, RP, at the bottom. BB and FC are in the Cape Foulweather region, SH and GH are in the Cape Perpetua region, BP, CB and RP are in the Cape Blanco region.

and equal variance by inspecting probability plots and *p*-values from Levene’s test for unequal variance.

We used multiple linear regression to test the response of algal cover to tidal height, barnacle cover, limpet density and site. All explanatory variables were significant, so backward elimination to fit a reduced model was unnecessary.

2.4.2. Grazing rate experiments

These experiments had two treatments, full enclosure (–limpet) and partial enclosure (+limpet). Response variables were percent cover of algae in each treatment. To test how actual grazing rate varied, we also tested the effect of region and zone on the difference between +limpet and –limpet treatments at the end of the

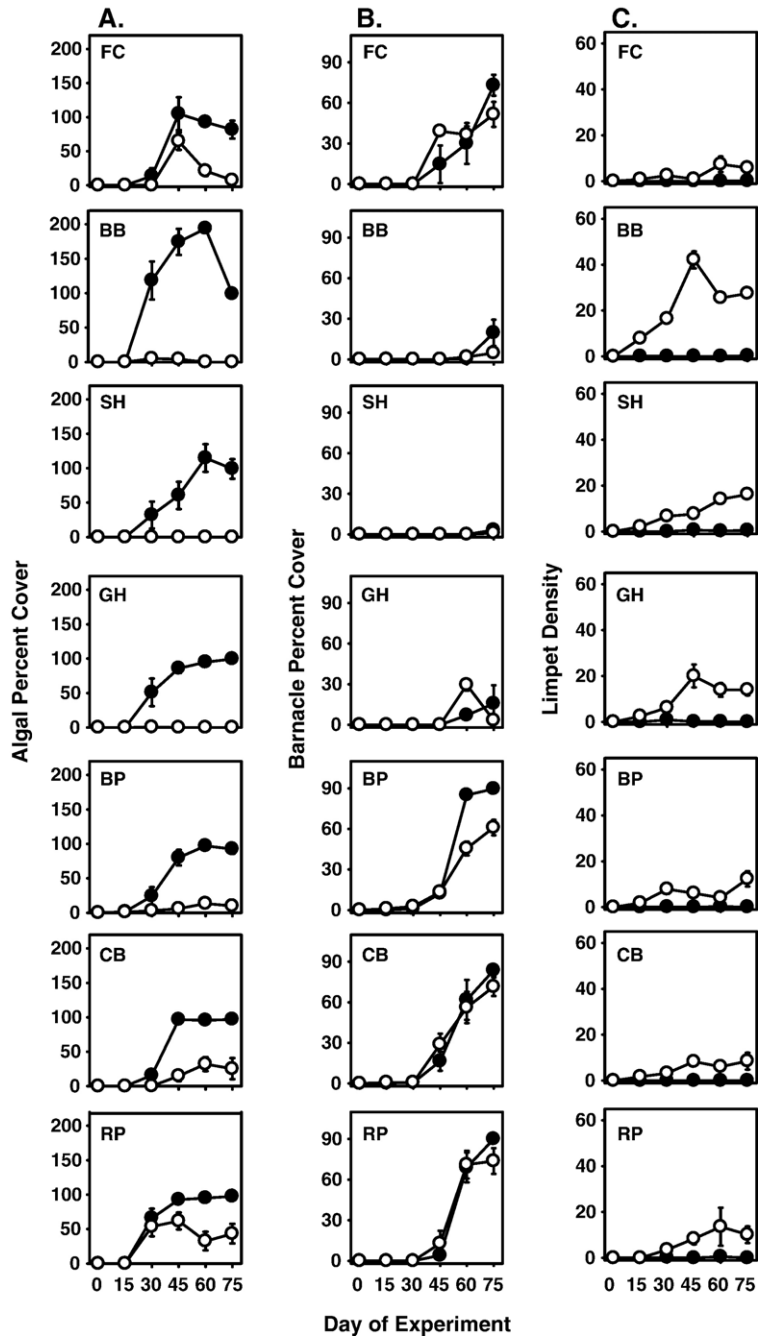


Fig. 8. Results of the mid zone herbivore effect experiment in 2000. See Fig. 7 caption for further detail.

experiment (day 30). Finally, as in grazer effect experiments, we used multiple linear regression to test the response of algal cover to zone (mid or low), barnacle cover, limpet density and site.

3. Results

3.1. Grazer effect experiments

3.1.1. Algal cover

The effects of grazers on cover of early successional algae varied at all scales (coast, region, site, zone). Between zones, overall grazer impacts in the low zone tended to be more spatially variable and weaker than were grazer impacts in the mid zone (compare Fig. 4A and B to C). In the low zone in 1999, grazer effects on algal percent cover varied differentially among sites through time (Figs. 5A and 6, Table 1: 1999, within

subjects; time × site × grazer interaction). In 2000, grazer effects were context-dependent, varying by region, zone and grazer presence, and by site within region through time (Figs. 7A, 8A, 9A,B, Table 1: 2000, within subjects; time × region × zone × grazing, and time × site nested within region interactions). In the low zone, grazing effects were greatest at SH and GH in both years (Figs. 4A and B, 5A, 7A). At the regional scale, low zone grazing effects at Cape Perpetua (CP) tended to be stronger than at Cape Foulweather (CF) to the north and Cape Blanco (CB) to the south (Figs. 6 and 9B; ranks based on linear contrasts, listed north to south, for 1999: CF < CP = CB and CF = CB, and for 2000: CF < CP > CB and CF = CB). At the coast (Central = C vs. South = S) scale, ranks were C = S (1999) and C > S (2000). The lack of clear region- and coast-scale differences in 1999 is likely due to lower site-level replication. Mid zone grazing effects varied less among

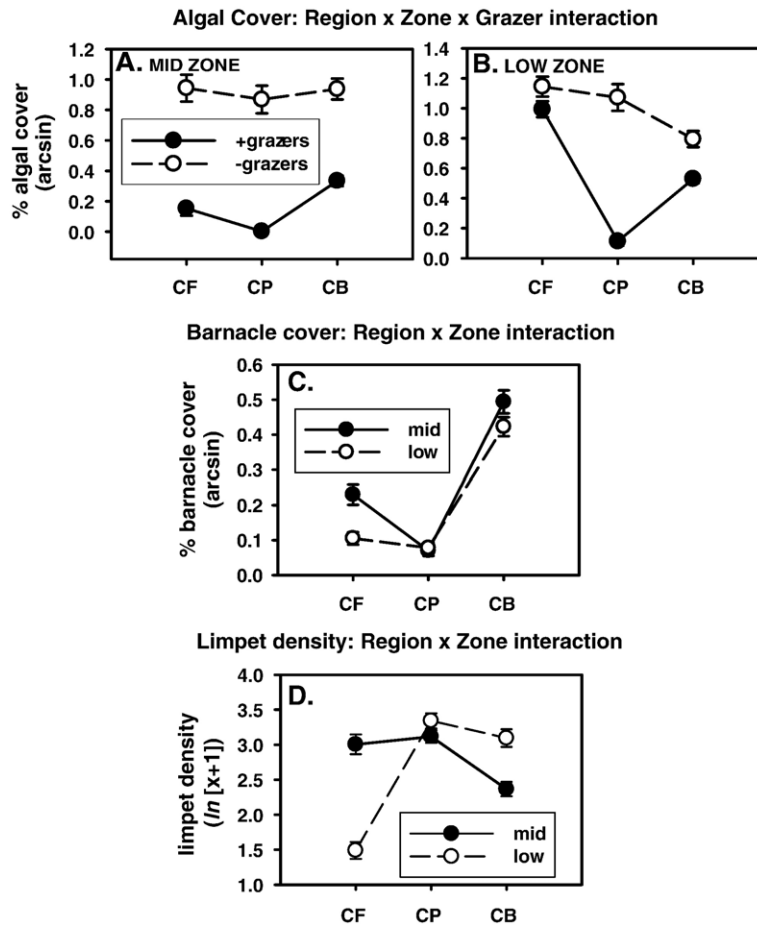


Fig. 9. Analysis of (A, B) the cape (=region) × zone × grazing treatment interaction for changes in algal cover, (C) the cape (=region) × zone interaction for changes in barnacle cover, and (D) the cape (=region) × zone interaction for limpet densities in +limpet plots in the 2000 grazing effect experiments. CF = Cape Foulweather; CP = Cape Perpetua; CB = Cape Blanco.

sites and capes than in the low zone but differences were evident (Figs. 4C, 8A, 9A). At the regional scale in the mid zone, among-cape ranks were $CF = CP > CB$ and $CF = CB$, and the coast scale, ranks were $C > S$.

Multiple linear regression indicated that zone, barnacle cover and limpet density affected the cover of algae in the effect experiments, and these relationships varied among sites. In the grazer effect experiment, zone ($p = 0.0002$), barnacle cover ($p = 0.031$), limpet density ($p < 0.0001$) and site ($p = 0.0011$) all contributed to variation in algal cover, explaining 40.9% of the variance.

In summary, grazer effects were greater on the central than the southern coast in 2000, but not in 1999. On average on the central coast, algal cover was 40% lower (= effect size; Table 2) in the presence vs. the absence of grazers in the low zone, while in the mid zone algal cover was 25% lower (Table 2). The smaller between-coast average effect size in the mid zone was due to the stronger effect of grazing in the south coast mid zone.

3.1.2. Initial algal accumulation rate

Clearance of the plots also removes the resident limpet population, and judging from when grazing effects appeared, their reinvasion of the +limpet plots generally takes about two (low zone) to four (mid zone) weeks. To test for among-site and among-region differences in initial microalgal abundance, we examined changes in initial algal accumulation in the most complete (2000) experiment, before limpets had invaded the +limpet plots. We reasoned that the initial (first two weeks) flush in algal growth, before grazing effects became strong, would be the best indicator of among-region and among-site differences in productivity. To be conservative, and to avoid confounding algal growth with grazing effects (as could occur in the –limpet plots), we examined changes in just the +limpet plots. In most cases, between-treatment differences did not emerge until day 30 or later (Figs. 7A and 8A).

In 2000 in the low zone, no algae had accumulated by day 15 at CP (sites SH and GH), while accumulations

Table 2

Results of linear contrasts on regional differences in the grazer effect and grazing rate experiments in the mid and low intertidal zones in 1999 and 2000

	Low 1999		Mid 1999		Low 2000		Mid 2000	
	Effect Size	95% CI	Effect Size	95% CI	Effect Size	95% CI	Effect Size	95% CI
Grazer effect experiments								
Grazer effects								
Central vs. Southern	ns	ns			40	12–68	25	6, 49
CF vs. CP	–36	–7, –65			–109	–72, –146	ns	ns
CF vs. CB	ns	ns			ns	ns	ns	ns
CP vs. CB	ns	ns			95	62, 128	32	8, 62
Barnacle cover								
Central vs. Southern					–40	–26, –54	–57	–50, –64
CF vs. CP					ns	ns	31	21, 41
CF vs. CB					–39	–23, –55	–41	–32, –50
CP vs. CB					–40	–24, –56	–72	–63, –81
Grazing rate experiments								
Grazing rate								
Central vs. Southern			–1.1	–0.5, –2.1	2.2	0.6, 3.8	1.5	0.9, 2.1
CF vs. CP			–3.0	–1.9, –4.1	–2.5	–0.7, –4.3	ns	ns
CF vs. CB			–2.8	–1.9, –3.7	ns	ns	1.7	1, 2.4
CP vs. CB			ns	ns	3.5	1.9, 5.1	1.4	0.7, 2.1
Barnacle cover								
Central vs. Southern					–42	–27, –57	–69	–61, –77
CF vs. CP					ns	ns	27	17, 37
CF vs. CB					–44	–26, –62	–55	–46, –64
CP vs. CB					–40	–22, –58	–83	–74, –92

For each response we examined four contrasts: central vs. southern coast and each pairwise comparison between Cape Foulweather (CF), Cape Perpetua (CP) and Cape Blanco (CB). Non-significant comparisons are indicated with “ns”. For each comparison we present the effect size, measured as difference in mean responses between regions, and the associated 95% confidence interval from the linear contrasts. Positive values indicate that the first region was greater than the second, while negative values indicate that the second region was greater. Grazer effect was the difference between the –limpet and +limpet plots. In both the effect and rate experiments, barnacle cover was measured as the average percent cover in the –limpet and +limpet plots. Grazing rate was the daily rate of loss of algae (percent cover) in the –limpet plots relative to the +limpet plots. *Per capita* effects were measured as the grazing rate divided by the average number of limpets in the +limpet plots.

Table 3

Results of repeated-measures ANOVA testing the effect of region and zone on barnacle cover in the 2000 grazer effect experiments

Univariate analysis					Multivariate analysis			
Source	<i>df</i>	<i>MS</i>	<i>F</i>	<i>p</i>	Wilks' λ	<i>df</i>	<i>F</i>	<i>p</i>
<i>Between subjects</i>								
Region	2	14.4949	134.6	< 0.0001				
Zone	1	1.2114	11.2	0.001				
Region*zone	2	0.3682	3.42	0.03				
Site (region)	4	2.2600	21.0	< 0.0001				
Error	200	0.1077						
<i>Within subjects</i>								
Time	4	8.7829	244.6	< 0.0001	0.27810	4,197	127.8	< 0.0001
Time*region	8	1.9252	53.6	< 0.0001	0.39199	8,394	30.4	< 0.0001
Time*zone	4	0.7711	21.5	< 0.0001	0.81026	4,197	11.5	< 0.0001
Time*region*zone	8	0.3176	8.84	< 0.0001	0.75524	8,394	7.42	< 0.0001
Time*site (region)	16	0.3961	11.0	< 0.0001	0.55003	16,602	8.14	< 0.0001
Error	800	0.0359						

Grazing treatment had no effect on barnacle cover. The sphericity test for multivariate normality failed ($\chi^2=302$, $p<0.0001$) so we adjusted the probabilities in the within-subjects test using the Greenhouse–Geisser epsilon (=0.69569).

Table 4

Results of repeated-measures ANOVA testing the effect of site (1999) and region and zone (2000) on limpet density in +limpet treatments

Univariate analysis					Multivariate analysis			
Source	<i>df</i>	<i>MS</i>	<i>F</i>	<i>p</i>	Wilks' λ	<i>df</i>	<i>F</i>	<i>p</i>
1999 Low zone								
<i>Between subjects</i>								
Site	4	25.5940	11.7	< 0.0001				
Error	55	2.1940						
<i>Within subjects</i>								
Time	1	4.9356	15.1	0.0003				
Time*site	4	4.5296	13.9	< 0.0001				
Error	55	0.3268						
2000 Low and mid zones								
Univariate analysis					Multivariate analysis			
Source	<i>df</i>	<i>MS</i>	<i>F</i>	<i>p</i>	Wilks' λ	<i>df</i>	<i>F</i>	<i>p</i>
<i>Between subjects</i>								
Region	2	53.4060	16.4	< 0.0001				
Zone	1	7.4957	2.30	0.13				
Region*zone	2	81.9584	25.1	< 0.0001				
Site (region)	4	31.4748	9.65	< 0.0001				
Error	129	3.2618						
<i>Within subjects</i>								
Time	4	72.5078	138.5	< 0.0001	0.23125	4,126	124.5	< 0.0001
Time*region	8	2.0627	3.94	0.0003	0.77978	8,352	4.17	0.0001
Time*zone	4	0.2915	0.56	0.67	0.98603	4,126	0.44	0.77
Time*zone*region	8	1.5313	2.93	0.005	0.81475	8,352	3.40	0.001
Time*site (region)	16	2.8235	5.39	< 0.0001	0.56368	16,385	4.97	< 0.0001
Error	516	0.5235						

In 1999, we analyzed data from 30 and 60 days only due to missing data at other sampling times. In 2000, the sphericity test for multivariate normality failed (Mauchly criterion; $\chi^2=77.4$, $p<0.0001$), so we adjusted probabilities in the within-subjects tests using the Greenhouse–Geisser epsilon (0.88033).

For the data in bold, significance was at $p<0.05$ or less.

were all >0 at both CF (FC and BB; $\text{mean} \pm 1 \text{ se} = 43.4 \pm 6.6\%$) and CB (BP, CB, RP; $15.9 \pm 2.4\%$ — Fig. 7A). Nested ANOVA (with region, treatment, and site (region) as main effects) indicates that algal cover varied by region and treatment ($p = 0.021$). At CF, cover in $-$ limpets plots was less than cover in $+$ limpet plots (linear contrasts, $p = 0.0005$) but algal cover did not differ between grazing treatments at the other capes (linear contrasts, $p \geq 0.5$). Region ranks of algal cover at day 15 were $\text{CF} > \text{CP} < \text{CB}$ and $\text{CF} > \text{CB}$. Site rankings were $\text{FC} < \text{BB} > \text{SH} = \text{GH} < \text{BP} = \text{RP} = \text{CB}$.

In the mid zone, algal accumulation was slower than in the low zone (Fig. 8A) so we focused on day 30. Nested ANOVA (with region, grazing treatment, and site (region) as main effects) indicates that algal cover varied by region and treatment ($p = 0.03$) with large differences between treatments at CF and CP (Fig. 8A, day 30; linear contrasts, $p < 0.0001$) and smaller differences between treatments at CB (Fig. 8A, day 30; linear contrasts, $p < 0.003$). Differences in algal accumulation in $-$ limpet plots did not differ among capes (linear contrasts, $p > 0.15$ or more). Region ranks were $\text{CF} = \text{CP} < \text{CB}$ and $\text{CF} = \text{CB}$, and coast ranks were $\text{C} < \text{S}$. Site rankings were $\text{FC} < \text{BB} > \text{SH} < \text{GH} > \text{BP} = \text{CB} < \text{RP}$ (from highest to lowest abundance, ranks were $\text{BB} > \text{RP} > \text{GH} > \text{SH} = \text{BP} = \text{CB} = \text{FC}$). Clearly, in the mid zone, among-site differences were unrelated to region. BB in the north and RP in the south stood out as sites of the greatest algal accumulation rates during early succession.

Thus, these data suggest that at least in the initial increase phase in the low zone, bottom-up effects tend to be greater at CF and weaker at CP. Early productivity at CB differed between years, and among-site differences were important, with BB consistently having the highest initial cover. In the mid zone, changes were slower and among-region differences were driven by site-specific differences that appeared unrelated to oceanography.

3.1.3. Barnacle cover

Barnacle cover was measured in the low and mid zone experiments in 2000. Data from sampling periods 1–3 in both the mid and low zone did not meet assumptions of normality, but when the design is balanced and sample size is large, ANOVA is robust to violations of this assumption so we performed the RM-ANOVA across all sample periods.

In 2000, barnacle cover varied among sites through time (Figs. 7B, 8B, Table 3, time \times site (region) interaction), and by region and zone through time (Fig. 9C, Table 3, time \times region \times zone interaction). By the end of the experiment, barnacle cover was highest on

the southern coast in both zones (Figs. 7B, 8B, 9C). Region ranks in the low zone were $\text{CF} = \text{CP} < \text{CB}$ and $\text{CF} < \text{CB}$ and in the mid zone were $\text{CF} > \text{CP} < \text{CB}$ and $\text{CF} < \text{CB}$ (Fig. 9C); coast ranks were $\text{C} < \text{S}$ in both zones (linear contrasts). Effect size was greater on the southern coast (57% cover) than on the central coast (40%), driven primarily by a nearly two-fold greater abundance of barnacles at CB (72%) than at CP (40%) (Table 2).

3.1.4. Limpet density

Paint barriers effectively excluded limpets (Figs. 5B, 7C, 8C). In both years and both zones, limpet abundance increased with time. This temporal pattern was likely due to limpet recruitment throughout the summer. In 1999 in the low zone, limpet abundance varied differentially among sites through time (Table 4, within subjects, time \times site interaction). In 2000, limpet abundance varied

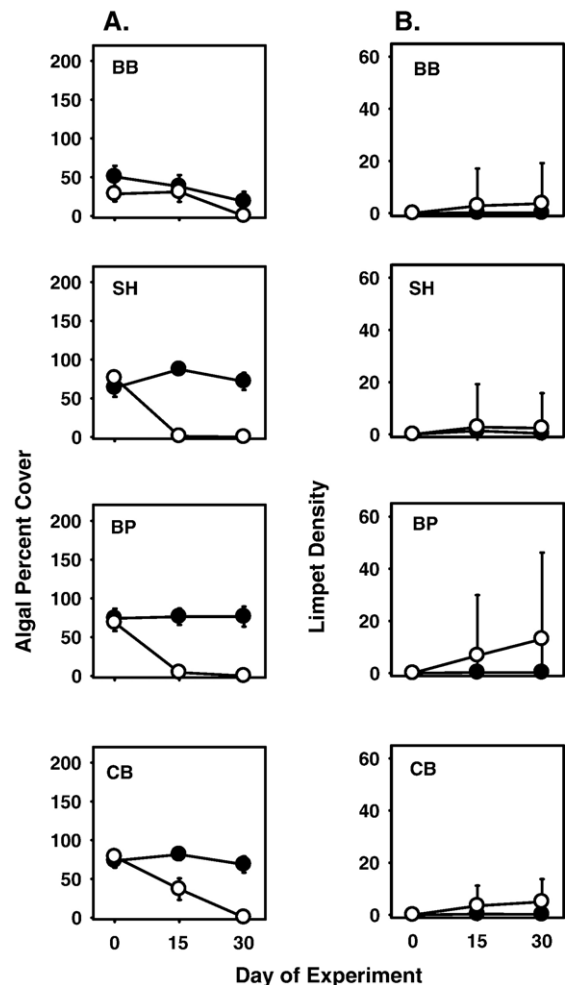


Fig. 10. Results of the mid zone grazing rate experiment in 1999. See Fig. 5 caption for further detail.

among regions between zones through time (Table 4, within subjects, time \times region \times zone interaction) and among sites (Table 4, within subjects, time \times site(region) interaction). In the low zone, limpet abundance was highest at SH, GH and BP (Fig. 7C), while in the mid zone abundance was highest at BB (Fig. 8C). Limpet abundance varied differentially among regions by zone, with higher densities in the mid zone at CF and CP and higher densities in the low zone at CP and CB (Fig. 9D).

3.2. Grazing rate

3.2.1. Algal cover

Results of grazing rate experiments were generally consistent with those of the grazing effect experiments. In 1999, algal cover in mid zone grazing rate exper-

iments varied among sites with the greatest effects observed at SH, BP and CB (Fig. 10A, Table 5). Region ranks were CF < CP = CB and CF < CB, and coast ranks were C < S (linear contrasts).

In 2000, algal cover in grazing rate experiments varied with region, zone and treatment through time (Figs. 11A and 12A; Table 5, within subjects, time \times region \times zone \times grazing interaction). In the low zone, the largest differences occurred at CP sites SH and GH (Fig. 11A). Region ranks were CF < CP > CB and CF = CB, and coast ranks were C > S (linear contrasts). In the mid zone, the largest differences occurred at central coast sites FC, BB, SH and GH (Fig. 12A). Region ranks were CF = CP > CB and CF > CB, and coast ranks were C > S. Interaction plots (not shown) for grazing rate experiments (between subjects: region \times zone \times grazing) were very similar to those for

Table 5

Results of repeated-measures ANOVA testing the effects of region, zone and grazing on algal cover in the grazing rate experiments in 1999 (mid zone) and 2000 (mid and low zones)

Univariate analysis					Multivariate analysis			
Source	df	MS	F	p	Wilks' λ	df	F	p
1999 Mid zone								
Between subjects								
Site	4	1.8578	6.14	0.0003				
Grazing	1	13.3623	44.2	<0.0001				
Site* grazing	4	0.6846	2.26	0.07				
Error	68	0.3025						
Within subjects								
Time	2	4.8497	67.4	<0.0001	0.36748	2, 67	57.7	<0.0001
Time* site	8	0.1258	1.75	0.09	0.80611	8, 134	1.91	0.06
Time* grazing	2	2.6834	34.3	<0.0001	0.49613	2, 67	34.0	<0.0001
Time* site* grazing	8	0.6432	8.94	<0.0001	0.47657	8, 134	7.51	<0.0001
Error	136	0.0719						
2000 Low and mid zones								
Between subjects								
Region	2	0.05320	0.33	0.72				
Zone	1	0.16379	1.02	0.31				
Grazing	1	14.81832	92.5	<0.0001				
Region* zone	2	3.01458	18.8	<0.0001				
Region* grazing	2	1.87885	11.7	<0.0001				
Region* zone* grazing	2	0.34378	2.15	0.12				
Site (region)	4	0.75714	4.73	0.001				
Error	125	0.16017						
Within subjects								
Time	2	4.88433	74.8	<0.0001	0.457136	2, 124	73.6	<0.0001
Time* region	4	0.38691	5.93	0.0004	0.782237	4, 248	8.10	<0.0001
Time* zone	2	0.15768	2.42	0.10	0.957166	2, 124	2.77	0.07
Time* grazing	2	6.96228	106.7	<0.0001	0.401305	2, 124	92.5	<0.0001
Time* region* zone	4	0.61564	9.43	<0.0001	0.802395	4, 248	7.21	<0.0001
Time* region* grazing	4	0.56443	8.65	<0.0001	0.784063	4, 248	8.02	<0.0001
Time* region* zone* grazing	4	0.19523	2.99	0.03	0.900667	4, 248	3.33	0.01
Time* site (region)	8	0.10418	1.60	0.14	0.898537	8, 248	1.70	0.1
Error	250	0.06526						

In the 2000 analysis, the sphericity test (Mauchly criterion) for multivariate normality failed ($\chi^2=26.7, p<0.0001$) so we adjusted probabilities using the Greenhouse–Geisser epsilon (0.8368821). The 1999 data passed the multivariate normality criterion (sphericity test, Mauchly criterion: $\chi^2=1.66, p=0.44$). For the data in bold, significance was at $p<0.05$ or less.

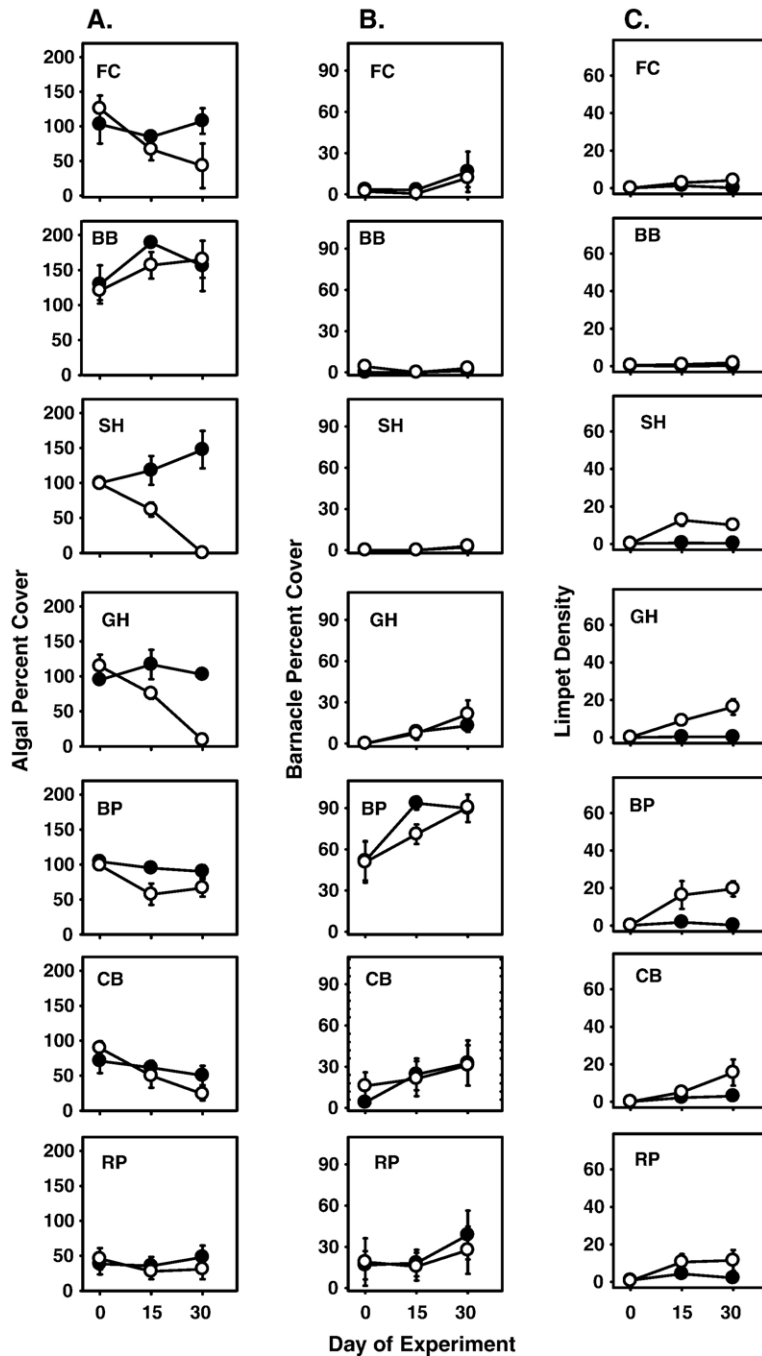


Fig. 11. Results of the low zone grazing rate experiment in 2000. See Fig. 7 caption for further detail.

grazing effect experiments (Fig. 9A,B), suggesting more uniform grazing rates across regions in the mid zone but higher rates at CP than at CF and CP. Analysis of actual grazing rates (not shown), as estimated by the difference between +limpet and -limpet treatments 30 days after initiation, yielded results identical to the above. In general,

CP tended to have larger impacts in grazing rate experiments than the capes to the north or south.

Multiple linear regression indicated that in the grazing rate experiment, zone ($p = 0.0052$), barnacle cover ($p = 0.026$), limpet density ($p < 0.0001$) and site ($p < 0.0001$) explained 47.9% of the variance in algal

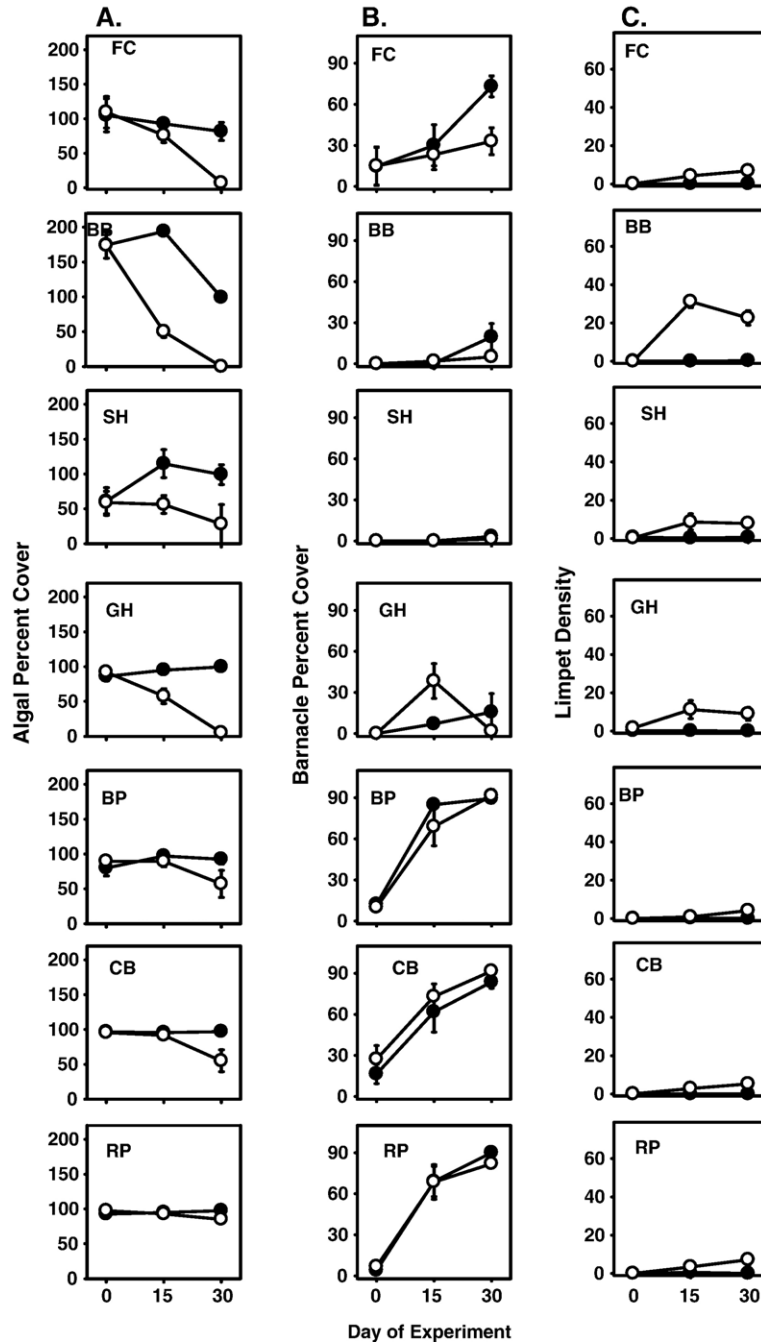


Fig. 12. Results of the mid zone grazing rate experiment in 2000. See Fig. 7 caption for further detail.

cover. Decreases in algal cover were associated with higher shore heights, higher barnacle covers, and higher limpet densities.

3.2.2. Barnacle cover

In 2000, barnacle cover in grazing rate experiments varied among sites within regions, and by region and

zone through time (Figs. 11B and 12B; Table 6, time by site (region) and time \times region \times zone interactions). Plots of the region \times zone interaction (not shown) were similar to those for grazer effects (Fig. 9C). In the low zone, region barnacle cover ranks were $CF = CP < CB$ and $CF < CB$, and coast ranks were $C < S$. In the mid zone, region ranks were $CF > CP < CB$ and $CF < CB$, and coast

Table 6

Results of repeated-measures ANOVA testing the effect of region and zone on barnacle cover in the 2000 mid and low zone grazing rate experiments

Univariate Analysis					Multivariate Analysis			
Source	df	MS	F	p	Wilks' λ	df	F	p
<i>Between subjects</i>								
Region	2	17.6654	134.3	<0.0001				
Zone	1	2.1277	16.2	0.0001				
Region*zone	2	0.5530	4.21	0.02				
Site (region)	4	2.1613	16.4	<0.0001				
Error	130	0.1315						
<i>Within subjects</i>								
Time	2	4.8207	115.0	<0.0001	0.33106	2,129	130.3	<0.0001
Time*region	4	0.8897	21.3	<0.0001	0.57141	4,258	20.8	<0.0001
Time*zone	2	0.7702	18.4	<0.0001	0.76291	2,129	20.0	<0.0001
Time*region*zone	4	0.3605	8.62	<0.0001	0.76800	4,258	9.10	<0.0001
Time*site (region)	8	0.1375	3.28	<0.0001	0.82149	8,258	3.33	0.001
Error	260	0.0418						

Grazing treatment had no effect on barnacle cover. The data passed the multivariate normality criterion (sphericity test, Mauchly criterion: $\chi^2=1.95$, $p=0.38$).

Table 7

Results of repeated-measures ANOVA testing the effect of site (1999, mid zone) and region and zone (2000, mid and low zones) on limpet density in +limpet treatments

Univariate analysis					Multivariate analysis			
Source	df	MS	F	p	Wilks' λ	df	F	p
1999 Mid zone								
<i>Between subjects</i>								
Site	4		3.6426				2.13	0.1
Error	34		1.7102					
<i>Within subjects</i>								
Time	1		0.8182				1.86	0.18
Time*site	4		1.5980				3.64	0.01
Error	34		0.4390					
2000 Low and mid zones								
Univariate analysis					Multivariate analysis			
Source	df	MS	F	p	Wilks' λ	df	F	p
<i>Between subjects</i>								
Region	2	5.9504	3.85	0.03				
Zone	1	0.0103	0.01	0.001				
Region*zone	2	16.4888	10.7	0.0001				
Site (region)	4	0.5940	0.38	0.82				
Error	60	1.5458						
<i>Within subjects</i>								
Time	2	142.2394	232.0	<0.0001	0.14474	2,59	174.3	<0.0001
Time*region	4	1.5391	2.51	0.06	0.79692	4,118	3.55	0.009
Time*zone	2	0.2591	0.42	0.66	0.98053	2,59	0.59	0.56
Time*zone*region	4	5.1303	8.38	<0.0001	0.71635	4,118	5.35	0.0005
Time*site (region)	8	0.3366	0.55	0.78	0.88515	8,118	0.93	0.50
Error	120	0.6121						

In 1999, no limpets were present in the +limpet treatments on day 0 so we analyzed only the day 15 and 30 results. In 2000, the sphericity test for multivariate normality failed (Mauchly criterion; $\chi^2=17.1$, $p=0.0002$), so we adjusted probabilities in the within-subjects tests using the Greenhouse–Geisser epsilon (0.79905).

ranks were $C < S$. On the southern coast, average barnacle cover in the low zone was 42% higher and in the mid zone was 69% higher than the central coast (Table 2).

3.2.3. Limpet density

Limpet density variation in the grazing rate experiment also was similar to that in the grazing effect experiments. Limpet density varied among sites in 1999, and by region and zone through time in 2000 (Figs. 11C and 12C, Table 7). Plots of the region \times zone interaction (not shown) were similar to those for grazer effects (Fig. 9D). In the low zone, region limpet density ranks were $CF < CP = CB$ and $CF < CB$, and coast ranks were $C = S$. In the mid zone, region ranks were $CF = CP > CB$ and $CF > CB$ and coast ranks were $C > S$.

4. Discussion

This study suggests that along a 260 km stretch of the Oregon coast, the impact of limpet grazers and the rate of grazing on early successional microalgae varies at all scales, from zone to site to region to coast. Coast- and region-scale variation was consistent with patterns of oceanographic conditions, zone-scale variation was likely influenced by differential grazer and algae responses to immersion time, and local site-scale variation appeared to be related mostly to local variation in limpet density.

4.1. Grazer effects and spatial scales

The impact of limpet grazers on the recolonization of bare space by algae varied between oceanographic regions in ways that were at least partly consistent with expectation (Question 1 from Introduction “were earlier between-site studies general?”). Previous studies at one site each on CF and CP (Menge, 2000) suggested the hypothesis that at sites in the low zone in regions with naturally higher abundances of macroalgae (i.e., CF and CB), grazer effects would be weaker than at sites in the region with low cover of algae (i.e. CP). This generally occurred in our low zone experiments.

When grazing interactions were examined across a wider range of scales, however (Question 2; “how do top-down effects vary across scales?”), a richer and more complex result emerged. In general, strong limpet effects on algal abundance occurred at site by zone combinations where limpet abundance was relatively high and either barnacle abundance was relatively low (e.g., SH and GH in low and mid zones, BB in mid zone; Figs. 7 and 8) or where algal colonization + growth was

relatively slow regardless of barnacle abundance (e.g., BP, CB, RP mid zones; Fig. 8). In contrast, weak limpet effects on algal abundance occurred at site by zone combinations where either limpet abundance was low (e.g., FC, BB in the low zone) or where barnacle abundance was relatively high (e.g., BP, CB, RP in the low zone). The exception to these groupings was the FC mid zone, where low densities of limpets had a relatively strong effect on algae despite relatively high abundance of barnacles. Thus, factors varying at regional (limpet density, algal colonization + growth) and coastal scales (barnacle cover), with sometimes substantial local-scale (site) variation (e.g., BB vs. FC) all contributed to grazing variation. Within-site (between-zone) variation was also important but not consistent among sites, regions or coasts. Within-zone variation across sites (e.g., low zone grazing effect and rate) indicates an interaction with other, region or coastal scale factors.

What are the likely underlying mechanisms? We consider four factors: direct effects of limpets, direct and indirect effects of barnacles, effects of immersion time, and oceanography-related interactions between benthic microalgae and shading by phytoplankton. First, consistent with previous studies (Dayton, 1971; Underwood, 1980; Branch, 1981; Hawkins and Hartnoll, 1983; Cubit, 1984; Dungan, 1986; Menge et al., 1999; Menge, 2000), limpet grazing controlled microalgal abundance in the mid zone at all sites and in the low zone at SH and GH. Second, limpets can interact with barnacles in at least two ways. During settlement of barnacles limpets reduce barnacle abundance through bulldozing (Dayton, 1971; Underwood et al., 1983; Farrell, 1991). After barnacles have established and grown to occupy a significant fraction of the space, however, they can inhibit limpet foraging (Choat, 1977) and provide safe microsites for algal colonization, thus indirectly increasing algal abundance despite the presence of a dominant grazer (Farrell, 1991). These latter effects seem most likely to be important determinants of the weak limpet effect in the low zone on the southern coast. Barnacle cover reached the highest levels in the low zone at these three sites, and limpet effects were weak even at BP where limpet densities were high (Fig. 7). Thus, the answer to Question 3 (“how do barnacles influence the limpet–microalgal interaction?”) is that barnacles generally inhibited limpet grazing, weakening their effect on microalgae.

Third, physical environmental factors seem likely to come into play when mid and low zone results are considered. Low zone habitats are immersed longer than are mid zone habitats, meaning that low zone algae

experience longer exposures to nutrients and less exposure to desiccating conditions and are thus likely to grow faster. Evidence of this can be seen in low and mid zone changes in algal abundance during the first two weeks of the experiments (Figs. 7A and 8A). In the mid zone, algal cover did not change from 0 during the first two weeks, while in the low zone algal after two weeks cover was >0 (16–43%) at all but Cape Perpetua sites. Under this scenario, bottom-up processes influencing algal abundance are generally likely to be stronger in the low zone than the mid zone. If so, then mid zone limpets may be more able to keep pace with algal colonization and growth, suggesting that top-down effects may dominate relatively uniformly in the mid zone, as was observed (Figs. 4C and 8A).

If greater immersion time had led uniformly to a predominance of bottom-up effects over top-down effects in the low zone, that is, if algal production outpaced the ability of limpets to consume them, then limpet effects would be uniformly weak in the low zone. This was not the case. Although such an effect may underlie the weak grazing effects seen in the low zone at Cape Foulweather (where in 2000 at least, low limpet densities were also a factor) and Cape Blanco regions, grazing effects were consistently strong in the low zone at sites in the Cape Perpetua region.

Question 4 asks “what are the effects on the limpet–microalgal interaction of oceanographic and other larger scale factors?” We suggest that variable oceanographic conditions help explain varying limpet–microalgal interaction strength in the low zone. As noted in the results, initial algal growth in our experiments at SH and GH was slow compared to other low zone sites. What might cause this differential result? Recent studies (K. Nielsen et al. unpublished data, M. Kavanaugh et al. unpublished data) suggest the hypothesis that dense phytoplankton blooms at SH and GH might shade benthic algae, slowing their growth. Simultaneous *in situ* quantification of phytoplankton concentration (using continuously measuring fluorometry) and of light (photosynthetically active radiation) in the low intertidal zone indicate that at high tide at SH, light can be completely attenuated during phytoplankton blooms (K. Nielsen et al. unpublished data). Such attenuation was not observed at FC. Long-term (~18 years) observations (B. Menge unpublished data, personal observations) indicate that dense phytoplankton blooms are common at CP sites and rare at CF sites during the upwelling (summer) season. Thus phytoplankton shading (an indirect bottom-up effect) may suppress micro- (and likely macro-) algal growth at CP, underlying the differential variation in grazing interaction strength in the low zone.

4.2. Grazing rates

Grazing rate experiments were carried out in an effort to reduce the effect of differential rates of colonization and growth that can occur in the limpet grazing effect experiments. We reasoned that by starting all experiments with similarly high initial algal cover (instead of starting at zero algal cover), differences in grazing would more truly reflect variation in top-down effects without confounding bottom-up differences.

In the low zone, grazing rates were generally consistent with results from the grazing effect experiments (Figs. 7 and 11). Sites that had the strongest grazing effects (SH, GH) also had the highest grazing rates. In this case, either low limpet density (FC, BB) or interference with grazing by barnacles (BP, CB, RP) seemed most closely associated with low grazing rates. High grazing rates at CP sites were associated with relatively high limpet densities and low barnacle cover, thus presumably allowing relatively unimpeded limpet foraging activity.

In the mid zone, grazing rates differed between 1999 and 2000 (Figs. 8 and 12). In 1999, rates were relatively high at CB, SH and GH and low at BB. In addition, the grazing rates at one site, CB, contrasted with the results of the grazing effect experiments (high rate, low effect). In contrast, in 2000, mid zone grazing rates were low at south coast sites and high at central coast sites (Fig. 12). As mentioned above, the high cover of barnacles on the southern coast in 2000 likely inhibited grazing by limpets. Although limpets can reduce barnacle cover by bulldozing newly settled cyprids (Farrell, 1991), in our rate experiments limpets were excluded from the plots for approximately one month. By the time the copper paint barriers were removed, barnacles had settled and grown to a size that afforded a refuge from bulldozing. Diatoms and algal sporelings that settled and grew on the barnacle tests were thus less accessible to limpets. The unusually strong grazing rates at FC seem due to high per limpet grazing effectiveness (high *per capita* grazing rates; data not shown), while the comparably high rate at BB apparently resulted from the exceptionally high limpet density that occurred at this site in this year (Fig. 12).

4.3. Resolving the paradox: Complex relationships between limpet grazers, barnacles and bottom-up influences

Question 5 asks “which model is most appropriate for this limpet–microalgal system; top-down control, bottom-up control, or coupled top-down/bottom-up

control?” Our analyses suggest that a coupled top-down/bottom-up model seems most applicable to limpet–microalgal food chains in this ecosystem, but that the nature of the coupling contrasted with that for predator–prey food chains. In the limpet–microalgal food chain, top-down effects were strong in the mid zone where bottom-up effects were generally weaker. In the low zone, interactions were more complex. Weak top-down effects in the low zone at CF and CB were related to stronger bottom-up effects, specifically, to an inability of limpets to keep pace with the rate of colonization and growth of microalgae. Modifying factors at some sites including barnacle inhibition of limpet grazers and perhaps also variable limpet recruitment and/or abundance. Strong top-down effects at CP were related to weaker direct bottom-up effects (microalgal colonization and growth), perhaps due to stronger indirect effects of phytoplankton shading, a bottom-up effect. Thus the balance between top-down and bottom-up effects on microalgae evidently generally varies inversely, but in a complex way with several processes that vary across a spectrum of spatial scales and environmental factors. Factors influencing the strength of this interaction varied on local to site to regional to coastal scales and included immersion time, varying limpet density, and oceanographic conditions. These dynamics contrast with those for predator–prey food chains along the Oregon coast. Predator–prey (sea star–mussel) interactions along the Oregon coast varied positively with higher predation occurring where recruitment of mussels and particulate food supply for filter feeders (mussels and barnacles) were higher (Menge, 1992; Menge et al., 1994, 2004; Menge, 2000).

Acknowledgements

We thank M. Hixon, J. Lubchenco, K. Nielsen, F. Ramsey, S. Shumway and four anonymous reviewers for helpful comments on earlier drafts. The research was supported by NSF Predoctoral and Ford Foundation Dissertation Fellowships (to T.L.F.), and grants from the Andrew W. Mellon Foundation, the David and Lucile Packard Foundation, and the Wayne and Gladys Valley Foundation (to B.A.M. and J. Lubchenco) and the University Research Innovation, Scholarship, Creativity Undergraduate Incentive Program (to A. S.). This is contribution number 249 from PISCO, the Partnership for Interdisciplinary Studies of Coastal Oceans, funded primarily by the Gordon and Betty Moore Foundation and David and Lucile Packard Foundation. [SS]

References

- Barth, J.A., Menge, B.A., Lubchenco, J., Chan, F., Bane, J.M., Kirincich, A.R., McManus, M.A., Nielsen, K.J., Pierce, S.D., Washburn, L., 2007. Delayed upwelling alters nearshore coastal ocean ecosystems in the northern California current. *Proceedings of the National Academy of Sciences of the United States of America* 104, 3719–3724.
- Benedetti-Cecchi, L., Cinelli, F., 1997. Confounding in field experiments: direct and indirect effects of artifacts due to the manipulation of limpets and macroalgae. *Journal of Experimental Marine Biology and Ecology* 209, 184–191.
- Bosman, A.L., Hockey, P.A.R., 1986. Seabird guano as a determinant of rocky intertidal community structure. *Marine Ecology Progress Series* 32, 247–257.
- Bosman, A.L., DuToit, J.T., Hockey, P.A.R., Branch, G.M., 1986. A field experiment demonstrating the influence of seabird guano on intertidal primary production. *Estuarine, Coastal and Shelf Science* 23, 283–294.
- Branch, G.M., 1981. The biology of limpets: physical factors, energy flow and ecological interactions. *Oceanography and Marine Biology Annual Reviews* 19, 235–379.
- Brink, K.H., 1983. The near-surface dynamics of coastal upwelling. *Progress in Oceanography* 12, 223–257.
- Bustamante, R.H., Branch, G.M., Eekhout, S., 1995a. Maintenance of an exceptional intertidal grazer biomass in South Africa: subsidy by subtidal kelps. *Ecology* 76, 2314–2329.
- Bustamante, R.H., Branch, G.M., Eekhout, S., Robertson, B., Zoutendyk, P., Schleyer, M., Dye, A., Hanekom, N., Keats, D., Jurd, M., McQuaid, C., 1995b. Gradients of intertidal primary productivity around the coast of South Africa and their relationships with consumer biomass. *Oecologia* 102, 189–201.
- Castenholz, R.W., 1961. The effect of grazing on marine littoral diatom populations. *Ecology* 42, 783–794.
- Choat, J.H., 1977. The influence of sessile organisms on the population biology of three species of acmaeid limpets. *Journal of Experimental Marine Biology and Ecology* 26, 1–26.
- Coleman, R.A., Underwood, A.J., Benedetti-Cecchi, L., Aberg, P., Arenas, F., Arrontes, J., Castro, J., Hartnoll, R.G., Jenkins, S.R., Paula, J., Santina, P.D., Hawkins, S.J., 2006. A continental scale evaluation of the role of limpet grazing on rocky shores. *Oecologia* 147, 556–564.
- Crowder, M.J., Hand, D.J., 1990. Analysis of repeated measures. Chapman and Hall, London.
- Cubit, J.D., 1984. Herbivory and the seasonal abundance of algae on a high intertidal rocky shore. *Ecology* 65, 1904–1917.
- Dahlhoff, E.P., Menge, B.A., 1996. Influence of phytoplankton concentration and wave exposure on the ecophysiology of *Mytilus californianus*. *Marine Ecology Progress Series* 144, 97–107.
- Dayton, P.K., 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* 41, 351–389.
- Dethier, M.N., Graham, E.S., Cohen, S., Tear, L.M., 1993. Visual versus random-point percent cover estimations: ‘objective’ is not always better. *Marine Ecology Progress Series* 96, 93–100.
- Dungan, M.D., 1986. Three-way interactions: barnacles, limpets, and algae in a Sonoran Desert rocky intertidal zone. *American Naturalist* 127, 292–316.
- Farrell, T.M., 1991. Models and mechanisms of succession: an example from a rocky intertidal community. *Ecological Monographs* 61, 95–113.
- Fraser, L.H., 1998. Top-down vs. bottom-up control influenced by productivity in a North Derbyshire, UK, dale. *Oikos* 81, 99–108.

- Fretwell, S.D., 1987. Food chain dynamics: the central theory of ecology? *Oikos* 50, 291–301.
- Hairston, N.G., Smith, F.E., Slobodkin, L.B., 1960. Community structure, population control, and competition. *American Naturalist* 94, 421–425.
- Hawkins, S.J., Hartnoll, R.G., 1983. Grazing of intertidal algae by marine invertebrates. *Oceanography and Marine Biology Annual Reviews* 21, 195–282.
- Hunter, M.D., Price, P.W., 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* 73, 724–732.
- Huyer, A., 1983. Coastal upwelling in the California Current system. *Progress in Oceanography* 12, 259–284.
- Kavanaugh, M.T., Menge, B.A., Nielsen, K.J., Goodrich, L.M., Chan F.T., Letelier, R.M., in preparation. Effects of changing phytoplankton productivity: are intertidal kelps light-limited?
- Kosro, P.M., 2005. On the spatial structure of coastal circulation off Newport, Oregon, during spring and summer 2001 in a region of varying shelf width. *Journal of Geophysical Research* 110. doi:10.1029/2004JC002769.
- Kosro, P.M., Barth, J.A., Strub, P.T., 1997. The coastal jet: observations of surface currents along the Oregon Continental Shelf from HF radar. *Oceanography* 10, 53–56.
- Leonard, G.H., Levine, J.M., Schmidt, P.R., Bertness, M.D., 1998. Flow-driven variation in intertidal community structure in a Maine estuary. *Ecology* 79, 1395–1411.
- Leonard, G.H., Ewanchuk, P.J., Bertness, M.D., 1999. How recruitment, intraspecific interactions and predation control species borders in a tidal estuary. *Oecologia* 118, 492–502.
- Leslie, H.M., Breck, E.N., Chan, F., Lubchenco, J., Menge, B.A., 2005. Barnacle reproductive hotspots linked to nearshore ocean conditions. *Proceedings of the National Academy of Sciences of the United States of America* 102, 10534–10539.
- Mann, K.H., Lazier, J.R.N., 1996. *Dynamics of marine ecosystems*, Second Edition. Blackwell Science, Cambridge.
- Meese, R.J., Tomich, P.A., 1992. Dots on the rocks: a comparison of percent cover estimation methods. *Journal of Experimental Marine Biology and Ecology* 165, 59–73.
- Menge, B.A., 1991. Generalizing from experiments: is predation strong or weak in the New England rocky intertidal? *Oecologia* 88, 1–8.
- Menge, B.A., 1992. Community regulation: under what conditions are bottom-up factors important on rocky shores? *Ecology* 73, 755–765.
- Menge, B.A., 2000. Top-down and bottom-up community regulation in marine rocky intertidal habitats. *Journal of Experimental Marine Biology and Ecology* 250, 257–289.
- Menge, B.A., 2003. The overriding importance of environmental context in determining the consequences of species deletion experiments. In: Levin, S.A., Kareiva, P. (Eds.), *The Importance of Species: Perspectives on Expendability and Triage*. Princeton University Press, Princeton, NJ, pp. 16–43.
- Menge, B.A., 2004. Bottom-up/top-down determination of rocky intertidal shorescape dynamics. In: Polis, G.A., Power, M.E., Huxel, G. (Eds.), *Food webs at the landscape level*. University of Chicago Press, Chicago, IL, pp. 62–81.
- Menge, B.A., Berlow, E.L., Blanchette, C.A., Navarrete, S.A., Yamada, S.B., 1994. The keystone species concept: variation in interaction strength in a rocky intertidal habitat. *Ecological Monographs* 64, 249–286.
- Menge, B.A., Daley, B.A., Wheeler, P.A., Dahlhoff, E., Sanford, E., Strub, P.T., 1997a. Benthic–pelagic links and rocky intertidal communities: bottom-up effects on top-down control? *Proceedings of the National Academy of Sciences of the United States of America* 94, 14530–14535.
- Menge, B.A., Daley, B.A., Wheeler, P.A., Strub, P.T., 1997b. Rocky intertidal oceanography: an association between community structure and nearshore phytoplankton concentration. *Limnology and Oceanography* 42, 57–66.
- Menge, B.A., Daley, B.A., Lubchenco, J., Sanford, E., Dahlhoff, E., Halpin, P.M., Hudson, G., Burnaford, J.L., 1999. Top-down and bottom-up regulation of New Zealand rocky intertidal communities. *Ecological Monographs* 69, 297–330.
- Menge, B.A., Sanford, E., Daley, B.A., Freidenburg, T.L., Hudson, G., Lubchenco, J., 2002. An interhemispheric comparison of bottom-up effects on community structure: insights revealed using the comparative-experimental approach. *Ecological Research* 17, 1–16.
- Menge, B.A., Lubchenco, J., Bracken, M.E.S., Chan, F.T., Foley, M.M., Freidenburg, T.L., Gaines, S.D., Hudson, G., Krenz, C., Leslie, H.M., Menge, D.N.L., Russell, R., Webster, M.S., 2003. Coastal oceanography sets the pace of rocky intertidal community dynamics. *Proceedings of the National Academy of Science, USA* 100, 12229–12234.
- Menge, B.A., Blanchette, C., Raimondi, P., Gaines, S., Lubchenco, J., Lohse, D., Hudson, G., Foley, M., Pamplin, J., 2004. Species interaction strength: testing model predictions along an upwelling gradient. *Ecological Monographs* 74, 663–684.
- Nielsen, K.J., 2001. Bottom-up and top-down forces in tide pools: test of a food chain model in an intertidal community. *Ecological Monographs* 71, 187–217.
- Nielsen, K.J., 2003. Nutrient loading and consumers: agents of change in open-coast macrophyte assemblages. *Proceedings of the National Academy of Science, USA* 100, 7660–7665.
- Nielsen, K.J., Menge, B.A., Grantham B.A., Lubchenco, J., in preparation. Light attenuation, upwelling, and community structure on rocky shores: can persistent phytoplankton blooms limit macrophytes?
- Oksanen, L., Fretwell, S.D., Arruda, J., Niemela, P., 1981. Exploitation ecosystems in gradients of primary productivity. *American Naturalist* 118, 240–261.
- Paine, R.T., 1984. Ecological determinism in the competition for space. *Ecology* 65, 1339–1348.
- Parrish, R.H., Nelson, C.S., Bakun, A., 1981. Transport mechanisms and reproductive success of fishes in the California Current. *Biological Oceanography* 1, 175–203.
- Phillips, N.E., 2002. Effects of nutrition-mediated larval condition on juvenile performance in a marine mussel. *Ecology* 83, 2562–2574.
- Phillips, N.E., Gaines, S.D., 2002. Spatial and temporal variability in size at settlement of intertidal mytilid mussels from around Pt. Conception, California. *Invertebrate Reproduction and Development* 41, 171–177.
- Polis, G.A., 1999. Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. *Oikos* 86, 3–15.
- Polis, G.A., Sears, A.L.W., Huxel, G.R., Strong, D.R., Maron, J., 2000. When is a trophic cascade a trophic cascade? *Trends in Ecology and Evolution* 15, 473–475.
- Rosenfeld, L.K., Schwing, F.B., Garfield, N., Tracy, D.E., 1997. Bifurcated flow from an upwelling center: a cold water source for Monterey Bay. *Continental Shelf Research* 14, 931–964.
- Sanford, E., Menge, B.A., 2001. Spatial and temporal variation in barnacle growth in a coastal upwelling system. *Marine Ecology Progress Series* 209, 143–157.
- Schmitz, O.J., Hamback, P.A., Beckerman, A.P., 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removal on plants. *American Naturalist* 155, 141–153.

- Smith, R.L., 1983. Circulation patterns in upwelling regions. In: Thiede, J. (Ed.), *Coastal Upwelling*. Plenum Publishing Corporation, pp. 13–35.
- Thompson, R.C., Norton, T.A., Hawkins, S.J., 2004. Physical stress and biological control regulate the producer–consumer balance in intertidal biofilms. *Ecology* 85, 1372–1382.
- Underwood, A.J., 1980. The effects of grazing by gastropods and physical factors on the upper limits of distribution of intertidal macroalgae. *Oecologia* 46, 201–213.
- Underwood, A.J., Denley, E.J., Moran, M.J., 1983. Experimental analyses of the structure and dynamics of mid-shore rocky intertidal communities in New South Wales. *Oecologia* 56, 202–219.
- von Ende, C.N., 1993. Repeated-measures analysis: growth and other time-dependent measures. In: Gurevitch, J. (Ed.), *Analysis of Ecological Experiments*. Chapman and Hall, New York.
- White, T.C.R., 2001. Opposing paradigms: regulation or limitation of populations? *Oikos* 93, 148–152.